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Sonne, Jesper

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High proportion of smaller-ranged hummingbird species coincides with ecological specialization across the Americas

Jesper Sonne[1], Ana M. Martín González[1,2], Pietro K. Maruyama[1,3], Brody Sandel[4], Jeferson Vizentin-Bugoni[1,3], Stefan Abrahamczyk[5,6] , Ruben Alarcón[7], Andrea C. Araujo[8], Francielle P. Araujo[3], Severino Mendes de Azevedo Jr[9], Andrea C. Baquero[1], Peter A. Cotton[10], Tanja Toftemark Ingversen[11], Glauco Kohler[12], Carlos Lara[13], Flor Maria Guedes Las-Casas[14], Adriana O. Machado[15], Caio Graco Machado[16], María Alejandra Maglianesi[17,18], Alan Cerqueira Moura[16], David Nogués-Bravo[1], Genilda M. Oliveira[19], Paulo E. Oliveira[15], Juan Francisco Ornelas[20], Licleia da Cruz Rodrigues[21], Liliana Rosero-Lasprilla[22], Ana Maria Rui[23], Marlies Sazima[24], Matthias Schleuning[17], Allan Timmermann[4], Isabela Galarda Varassin[25], Zhiheng Wang[1, 26], Stella Watts[27], Jon Fjeldså[1], Jens-Christian Svenning[4], Carsten Rahbek[1,28], Bo Dalsgaard[1]

[1]Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Univ. of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark.

[2]Pacific Ecoinformatics and Computational Ecology Lab, 1604 McGee Ave, 94703 Berkeley, California, USA.

[3]Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas (UNICAMP), Cx. Postal 6109, Campinas, SP 13083-865, Brazil.

[4]Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark

[5]Nees Institute of Plant Biodiversity, Meckenheimer Allee 170, 53115 Bonn, Germany.

[6]Institute of Systematic Botany, Zollikerstr. 107 Zurich, Switzerland.

[7]Biology Program, California State University Channel Islands, 93012 Camarillo, California,

USA.

[8]Centro de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso do Sul, 79070-900, Campo Grande, Mato Grosso do Sul, Brazil.

[9]Department of Biology, Rural Federal University of Pernambuco, Recife, Pernambuco, Brazil.

[10]Marine Biology & Ecology Research Centre, Plymouth University, Plymouth PL4 8AA, UK

[11]Stationsvej 33, DK-6580 Vamdrup, Denmark.

[12]Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Petrópolis, CEP 69080-971, Manaus, Amazonas, Brazil.

[13]Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala. Km 10.5 Autopista Tlaxcala-San Martín Texmelucan, San Felipe Ixtacuixtla, 90120, Tlaxcala, Mexico.

[14]Department of Zoology, Federal University of Pernambuco, Recife, Pernambuco, Brazil.

[15]Instituto de Biologia, Universidade Federal de Uberlândia -UFU, Uberlândia, Minas Gerais, Brazil.

[16]Laboratório de Ornitologia, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana, 44036-900, Bahia, Brazil.

[17]Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt (Main), Germany.

[18]Vicerrectoría de Investigación. Universidad Estatal a Distancia (UNED), San José, Costa Rica.

[19]Instituto Federal do Triângulo Mineiro, Campus Uberlândia, Uberlândia, Minas Gerais, Brazil.

[20]Departamento de Biología Evolutiva, Instituto de Ecología AC, Carretera antigua aCoatepec 351, El Haya, Xalapa, Veracruz 91070, Mexico.

[21]Laboratory of Ornithology, Department of Zoology, ICB, Minas Gerais Federal University, Post office box 486, 31270-901, Belo Horizonte, Minas Gerais, Brazil.

[22]Grupo de Investigación Biología para la Conservación, Escuela de Ciencias Biológicas, Universidad Pedagógica y Tecnológica de Colombia, Colombia.

[23]Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Universidade Federal de Pelotas, Capao do Leao, Rio Grande do Sul, Brazil.

[24]Departamento de Biologia Vegetal, Universidade Estadual de Campinas (UNICAMP), Cx. Postal 6109, Campinas-SP, 13083-970, Brazil.

[25]Laboratório de Ecologia Vegetal, Departamento de Botânica, Universidade Federal do Paraná, 81531-980 Curitiba, Paraná, Brazil.

[26]Department of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China.

[27]Landscape and Biodiversity Research Group, Department of Geographical and Environmental Sciences, University of Northampton, Avenue Campus, St George's Avenue, Northampton NN2 6JD, UK.

[28] Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK.

Corresponding author: Jesper Sonne, Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Univ. of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark, Phone: +4526330554, jsonne@snm.ku.dk

Abstract

Species communities that experience stable conditions have been speculated to preserve more specialized interspecific associations as well as having higher proportions of smaller-ranged species. However, this suggestion remains poorly supported with empirical evidence. Here, we analyzed data for hummingbird resource specialization, range size, contemporary climate and late Quaternary climate stability for 46 hummingbird-plant mutualistic networks distributed across the Americas, representing 130 hummingbird species (ca. 40% of all hummingbird species). We demonstrate a positive relationship between the proportion of smaller-ranged hummingbird species (SRS) and community-level specialization, i.e. the division of the floral niche among coexisting hummingbird species. This relationship remained strong also when accounting for climate. Furthermore, the much stronger statistical effect of SRS on specialization than *vice versa* (standardized coefficient = 0.75 *vs.* 0.43), suggests that climate largely associates with specialization through species' range-size dynamics. Irrespective of the exact mechanism involved, our results indicate that communities consisting of higher proportions of smaller-ranged species may be vulnerable to disturbance not only because of their small geographic ranges but also because of high degree of specialization.

Keywords: biogeography, climate gradients, macroecology, mutualistic networks, range size, specialization

1. Introduction

Ecological specialization may facilitate species coexistence and speciation, and is therefore hypothesized to structure global patterns of biodiversity [1]. Notably, higher degrees of community-level resource specialization, i.e. the division of local resources, may be associated with reduced interspecific competition and greater local richness [2]. It is therefore debated whether high ecological specialization in the tropics may contribute to the observed continental-scale increased species richness toward the tropics [3–10]. Likewise, it is speculated that large-scale geographical differences in ecological specialization coincides with patterns of range-size frequency distributions [11].

We address this and the role of extrinsic factors, notably climate, as potential determinants of community-level specialization and range-size distributions. Contemporary climate has been suggested to influence ecological specialization, with communities in productive areas having the highest degree of specialization [12,13]. Similarly, in areas with low contemporary seasonality, where resource availability supposedly is relatively stable throughout the year, communities may have a higher degree of specialization than those found in more seasonal environments [14–16]. Recent studies have also pointed towards historical climate fluctuations as influencing the local degree of specialization, as unstable climatic conditions are hypothesized to disrupt specialized species interactions, either through changes in the phenology of species or through increased dynamics in range-size [6,11,17–19]. Both ecological and historical factors may thus shape geographical patterns of ecological specialization as found for plant-hummingbird networks, which have a higher community-wide specialization in areas with higher precipitation and temperature, lower seasonality and more stable climate conditions since the last glacial maximum [6,20]

Contemporary and historical climate may also affect the geographical distribution of species range-sizes [21–23]. For instance, variable climate conditions have traditionally been

suggested to select for broad environmental tolerance, which influence the potential geographical range of species and, hence, causes species to have large ranges in seasonal areas [23–27], though see [28,29]. A highly seasonal climate may also force species to migrate in order to track suitable environmental conditions, and as smaller-ranged species have been suggested to have weaker dispersal ability than larger-ranged species [30], they are more likely to be residents in seasonally stable environments. This reasoning may be extended to fluctuations in historical climate, which may have forced species either to adapt to the new conditions, track suitable climatic conditions or to go locally extinct. As smaller-ranged species may track suitable climate conditions more slowly [30], these would suffer from an increased local extinction probability under climate change [27,31]. In accordance with this, late Quaternary climate-change velocity correlates negatively with the global distribution of proportionally smaller-ranged amphibian, mammal and bird species [31].

Taken together, numerous studies have pointed towards historical climate stability and contemporary seasonality as being important to support both ecological specialization and high proportions of smaller-ranged species. Thus, areas with disproportionally many smaller-ranged species are expected to coincide geographically with a high degree of community-level ecological specialization, but this remains poorly supported [6,11,19]. We tested this using a database consisting of 46 quantitative hummingbird-plant networks, i.e., studies of all hummingbird species' visitation frequencies on plant species at a given locality. The 46 networks are distributed widely across the American mainland [20; figure 1]. Specifically, we investigate: (*i*) whether specialization in plant-hummingbird networks is positively related with community-level proportion of smaller-ranged species (hereafter SRS), and (*ii*) whether contemporary and late Quaternary climate correlates with both specialization and SRS, or whether contemporary and late Quaternary climate are more likely to influence specialization indirectly via SRS (or *vice versa).* Hummingbirds are well-suited for such large-scale comparative studies on the pattern of ecological specialization

as they are highly specialized on nectar-feeding, and the hummingbirds and the plants they pollinate are mutually dependent [32–34], i.e. it is ecologically relevant to understand how specialization vary geographically [6] Moreover, hummingbirds are highly successful, being the second most species-rich family of birds and able to thrive in an array of environments across most of the Americas [35], and, finally, hummingbird-plant communities have long served as model system for examining ecological and evolutionary processes as determinants of ecological specialization at the community-level [6,32,33]. Our study advances the current understanding of how geographical patterns of range-size and specialization are shaped, and have additional implications for conservation of species communities engaged in specialized associations.

2. Materials and Methods

(a) Plant-hummingbird network data.

We used a database consisting of 46 plant-hummingbird networks [table S1; see 20 for more detailed information about the network data], from which we constructed weighted interaction networks for the hummingbirds and their associated nectar plants (figure 1). Taking a network approach allow for detailed information about the interaction frequencies between all hummingbird and plant species within a given community to be summarized by easily interpretable metrics. For the present study, networks were presented as P (number of plant species) x H (number of hummingbird species) matrices with entries indicating the strength of each interaction (i.e. the number of visitations recorded for a given hummingbird-plant species pair). Known incidents of nectar robbing, for instance if a hummingbird pierced the flower corolla without contacting the floral reproductive organs, were not considered since they represent antagonistic rather than mutualistic interactions [36]. For a network to be included in the study, it should fulfil certain criteria: i) each study must have a community approach, i.e. aiming to include all hummingbird and

hummingbird-pollinated plant species within the given community over the sampled period; (ii) networks need to consist of weighted data, i.e. include frequency of interactions, since binary networks exhibit high sensitivity to sampling effort and species abundance [37]; (iii) moreover, island networks were not included since species from islands are naturally constrained in their geographic distribution by the hard boundaries made up by the sea. Measuring species range size solely as the number of occupied grid cells would therefore contain less biological and mostly geographical information and, hence, is not comparable to the situation on the continent.

(b) Measuring hummingbird range-size proportions.

The geographical range-size of each hummingbird species was extracted from an updated database previously presented in Rahbek & Graves [38] – see [39,40] for details on method and data sources. As an estimate of hummingbird geographical range-size, we used the total number of occupied $1^{o}\times 1^{o}$ latitude-longitude grid cells. Following Jetz and Rahbek [41], we divided the total number of species (n = 130) into quartiles according to range size (i.e. the 1^{st} quartile consists of the 25% species with the smallest ranges (n = 33) and the 4^{th} quartile consist of the 25% with largest ranges sizes in order to determine the community level proportion of smallest-ranging species (SRS). For each network, we calculated the proportion of 1^{st} quartile species. As larger-ranging species contribute with more records among communities than smaller-ranging species [41], even though the majority of hummingbirds have relatively small ranges (S1). Hence, summary statistics as the mean and median range size for co-occuring species would largely be influenced by large-ranging species. This was confirmed for data set where linear models regressing the local proportion of 25% of species with largest ranges, was strongly correlated with both the mean range size (Pearson correlation = 0.85, $P < 0.001$) and the median range size (Pearson correlation = 0.83, $P < 0.001$). On this basis, we assess the proportional variable SRS to be a more appropriate attribute of the local

range-size frequency distribution for determining the variation in presence of smaller-ranged species. In addition, where richness of smaller-ranged species may reflect areas of high stability [42,43], richness of larger-ranged species, which would influence the mean/median calculations, may rather reflect factors related to productivity [41]. Hence, for the reason that the degree of specialization may be higher in climatic more stable areas, we argue that testing for an association to the proportion of smaller-range species is more relevant. However, It should be noted that the range-size-frequency-distribution of our data is somewhat skewed toward larger ranges than the RSFD of all hummingbird species of the world (figure S1). This is why we refer to 1st quartile species as "smaller-ranged" species rather than using the term "restricted-range" species as in Jetz & Rahbek [41] and others using continental data on all species (see also "Sensitivity Analyses" below). This proportional variable was transformed by using arcsine square-root transformation for the further analysis.

(c) Specialization, richness, environmental variables and sampling intensity.

Following Blütgen, Menzel & Blütgen [44] ecological specialization (<d'>) for each hummingbird community was calculated as the weighted mean of the normalized Kullback-Leibler distance for all coexisting hummingbird species [45]. The estimate is based on frequency data representing the strength of each interaction (i.e.number of visits recorded for each hummingbird-plant partner) in the network, which has been shown to be relatively insensitive to sampling intensity and network size [44,46]. First, species level degree of specialization (d_i) is calculated as a comparison of the distribution of hummingbird interactions with plant partners in relation to the overall partner availability:

$$d_i = \sum_{j=1}^{c} \left(p'_{ij} \times ln \frac{p'_{ij}}{q_j} \right)$$

Here, p_{ij} is the proportion of interactions with plant *j* in relation to the summed number of interactions for hummingbird *i* (A_i), q_j denotes the summed number of interaction for plant *j* relative to the summed number of interactions in the network (*m*) and *c* indicates the plant species richness. Following a normalization procedure, letting d'_i denote the deviation of the empirical frequencies of interaction for hummingbird *i* from the null expectation that all plants a visited equal to their availability (see [44] for details regarding the normalization procedure), the weighted averaged degree of specialization for the hummingbird assembly is calculated as:

$$\langle d'_i \rangle = \frac{1}{m} \sum_{i=1}^{r} (d'_i \times A_i)$$

Where r denotes the hummingbird species richness. The index ranges between 0 (extreme generalization; i.e. many interactions with many plants shared by other hummingbird species) and 1 (extreme specialization; i.e. many interactions with few plants and limited sharing with other hummingbird species). Weighting the averages by the summed number of interactions for each hummingbird gives more accurate measures for comparison as rare interactions are not over-interpreted [44]. Conceptually, the use of $<d'_i>$ as a measure of ecological specialization can be translated into the functional attributes specific to the local species community, i.e. the realized Eltonian niche [47]. Estimating ecological specialization based on species interaction networks could potentially be biased by differences in species abundance. This is the reason for weighting the average degree of hummingbird specialization by the marginal sum of interactions, assuming a positive association between abundance and visitation frequency. Although we do not have sufficient independent measurement of abundance to validate this assumption, a study conducted on a network collected in the Brazilian Atlantic Rainforest documented that the frequency of hummingbird interactions was a good surrogate for their abundance [see Table S1 network ID 41 48]. On the other hand, for the specialization estimate, we identified potential confounding effects:

235 network size [6], i.e. the richness of hummingbird and plant species in the network (standardized
236 coefficient; *std. coeff.* = -0.495, P = 0.015), and network asymmetry [49], i.e. the ratio between the
237 richness of hummingbird and plant species P = 0.013). We thus conducted independent analyses
238 using the residuals of linear regressions predicting <d'> by respectively network size and network
239 asymmetry, respectively. To assess the confounding influence of differences in sampling effort, we
240 conducted additional linear regressions predicting both SRS and specialization by sampling
241 intensity, which for each network is calculated by dividing the total number of observed interactions
242 (square root transformed) with the richness for plants and hummingbirds [50].
243 The contemporary climate variables hypothesized to predict specialization and SRS,
244 i.e. mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality
245 (i.e. standard deviation in annual temerature; TS) and precipitation seasonality (i.e. standard
246 deviation in annual precipitation; PS), were extracted from the WorldClim database in resolution of
247 1 x 1 km [http://www.worldclim.org; 51]. We estimated variables reflecting historical climate
248 change as the absolute difference in temperature and precipitation between pre-industrial time and
249 the Last Glacial Maximum (21,000 years ago), i.e. temperature and precipitation anomalies
250 (AnomT and AnomP). To generate projections of climate anomaly, we used the Hadley Centre
251 Model Version 3 (HadCM3) at 3.75 x 2.5 arc degrees resolution and subsequently down scaled to
252 0.1 x 0.1 arc degrees [52]. We included also measures of topographic heterogeneity (i.e. range in
253 elevation; TH), as predictors of both specialization and SRS [53,54]. As an estimate of the
254 interactive effect of historical climate and topography, we included estimates of temperature and
255 precipitation velocity (VelT and VelP), which capture the buffering effect in mountain areas where
256 species can track their original climate zone by migrating a short distance up or down slope [55].
257 For each community, TH and estimates of historical and contemporary climate were calculated as
258 the average of values within a radius of 10 km from the sampled location. Given the large

geographical scale of the data, we assume that the regional down scaled climate estimates are good indicators of the variation of local climate among communities. To meet statistical assumptions about normality, mean annual temperature was squared and mean annual precipitation, temperature seasonality, temperature and precipitation velocities and anomalies were log-transformed prior to further analyses. All variables were scaled to zero mean and unit variance.

(d) Structural Equation Modeling.

Structural Equation Models (SEMs) are statistical tools used to evaluate multivariate hypotheses. Compared to multiple regression models, the main advantage is that they seek to account for both direct and indirect effects among predictor and response variables while allowing multiple dependent variables to be tested simultaneously. Initially, we constructed two SEM's based on *a priori* hypotheses, considering different causal paths among the response variables. The first considered a link from SRS to specialization, corresponding to a scenario where local preservation of higher proportions of smaller-ranged species (e.g. through lowered range size dynamics) affect species possibilities to develop specialized interactions in the local plant community. Secondly we considered an opposite link from specialization to SRS corresponding to a scenario where local opportunities to develop increased ecological specialization provides better conditions for the preservations of smaller ranged species. Due to relatively low sample size (n = 46) in comparison to the number of predictor variables, this model was simplified through model selections using the Akaike Information Criterion (AIC). For each response variable, among all model combinations, only predictors present in the better predicting models (determined from having ΔAIC less than 2 in relation to the model with lowest AIC; 50) were included in the initial SEM models (figure S2). The two SEMs were evaluated through the chi-square test, comparative fit index (CFI) and the Root Mean Square Error of Approximation (RMSA) [57]. The chi-square value indicates the divergence

between the sample and the fitted structures in the data and was used to evaluate overall model fit where a non-significant result (P> 0.05) indicated good model fit. The CFI compares the chi-square of the model with the chi-square value of an independent model assuming no correlation among all variables while accounting for sample size. With a range from 0 to 1, we accepted models with CFIs > 0.09 [58]. Lastly, the RMSA was implemented, but only on the simplified models due to the index's sensitivity to the number of estimated parameters in the model. Here, values below 0.07 were used as indication of good model fit [58]. We expected some degree of correlation among the included climate predictors. In order to obtain reliable model fit according to the three above mentioned indices, we identified and added this covariance based on high modification indices and large residual correlations [59,60]. By stepwise refitting, we simplified the SEMs, removing non-significant links conditional on the model fit being satisfied [61,62]. The contribution of each predictor variable was evaluated through the standardized path coefficients. Three additional SEM pairs were constructed to examine if our results were sensitive to the significant positive effects of network size and network asymmetry on specialization (figure S3-S4), and when using climate velocities rather than anomalies (figure S5). All SEMs were constructed and analyzed with the R package lavaan [63].

(e) Spatial auto-correlation.

Using the R package ncf [64], we assessed whether significant positive spatial autocorrelation occurred in linear model residuals by computing correlograms with distance classes of 1000 km. Four linear models were set up similarly to the direct links between climate and specialization and SRS as in figure. 2. None of them contained significantly positive spatial autocorrelation, and we thus conclude that spatial autocorrelation is negligible for the model results.

(f) Sensitivity analyses of range-size definition.

To evaluate the robustness to the use of different range-size cut-offs, We fitted ten additional linear models using different range-size cut-offs to define a smaller-ranged species (i.e. from 20 to 30% of species having the smallest range sizes; figure S6). In addition, we conducted follow up analyses using a redefined measure of the proportion of smaller-ranged species based on the 1^{st} quartile species of the global pool of mainland hummingbird species (n = 318) as in Jets, Rahbek & Colwell [43] rather than the one in our data set (n = 130). Following this method, a species was assigned to be smaller-ranged if it had a global range-size less than 10 grid cells, as this represent the threshold between 1^{st} and 2^{nd} quartile of the global species pool. For the 130 species occurring in the dataset, this cut-off will include the 13% of species with the smallest range sizes. Du to zero inflation in the corrected SRS variable, we were unable to conduct the above SEMs, which are based on linear model assumptions. Instead, we used a logistic regression including all data points (n = 46) to test the association between specialization on the corrected SRS (figure 3a). We note that a chi-square test applied on the residual deviance and degrees of freedom to assess model fit indicated that SRS was acceptably represented by a binominal distribution (P = 0.06). Considering specialization as response variable, we separated the corrected SRS into two variables: one categorical that simply determines whether communities hold smaller-ranged species or not (n = 46) and one containing only communities having smaller-ranged species according to the corrected threshold (n = 10). The association between the corrected SRS and specialization was fitted using ANOVA and simple univariate linear models, respectively (figure 3b and c).

In addition to the threshold used to define smaller-ranged species, the latitudinal variation in continental or biome narrowness may constitute hard boundaries to the range size of species [28,65]**,** which could also influence the association between SRS and specialization. To account for this, we used dispersion fields to construct a null model, which generates SRS values for each community from a similarity-weighted species source pool [66]. The null model integrates

data of the presence-absence of all 318 hummingbird species across mainland Americas at $1^{o} \times 1^{o}$ latitude-longitude resolution. The concept of the biogeographical sourse pool is based on dispersal of species to most likely occur within their biogeographical region [66,67]. Thus, we determined the regional source pool of a community using the rationale that species living in communities with species compositions more similar the focal are more likely to constitute its source pool. Across 1000 iterations of each community containing n species, the null model algorithm randomly samples n grid cells probabilistically weighted by the number of shared species with the focal community. From these, n species were randomly assembled weighted by their frequency of occurrence in the n sampled grid cells. For these, the null values of SRS were then calculated. Deviations between the observed SRS values and the normal curve of the null generated SRS values were standardized as the z-score: $\mathrm{SRSz} = (\mathrm{SRS}_{\mathrm{observed}} - \overline{\mathrm{SRS}_{\mathrm{null}}})/\mathrm{sd}(\mathrm{SRS}_{\mathrm{null}})$.

3. Results

We found a positive correlation between specialization and SRS (coefficient; *coef.* = 0.394, R^2 = 0.349, $P < 0.001$, $n = 46$). For the SEM containing a hypothesized direct link from specialization to SRS was considered, a positive association was found between the two (*std coeff.* = 0.43, figure. *2a*). Here, we found that SRS was negatively associated with temperature seasonality (TS; *std coeff.* = -0.42) and positively associated with topographical heterogeneity (TH; *std coeff.* = 0.42) and temperature anomaly (AnomT; *std coeff.* = 0.23), whereas specialization was negatively related to temperature anomaly (AnomT; *std coeff.* = -0.37) and positively related to both mean annual precipitation (MAP; *std coeff.* = 0.31) and precipitation anomaly (AnomP; *std coeff.* = 0.35). In the SEM having SRS as a predictor of specialization (figure *2b*), there was a similarly strong positive link from SRS to specialization (*std coeff.* = 0.75). In comparison to the above SEM, we here found

additional links between specialization and mean annual temperature (MAT; *std coeff.* = 0.29), TS (*std coeff.* = 0.31) and a positive influence of AnomP on SRS instead of specialization.

Linear regressions testing the influence of sampling intensity on specialization and SRS showed no significant associations (c*oef.* = -0.01, R^2 = 0.07, P = 0.07, n = 46; c*oef.* = -0.02, R^2 = 0.08, P = 0.06, n = 46 respectively). Similarly, the strong association between SRS and specialization was insensitive to specialization estimates when correcting for network richness (figure S3) and network asymmetry (figure S4). The results from the SEM pairs considering the interactive effect of topographic heterogeneity and historical climate through estimates of climate-change velocity also showed similar results (figure S5).

Linear regression including SRS variables calculated using different range-size cut-offs to define smaller-ranged species (ranging from 20% to 30% of species having the smallest range sizes) documented a robust association between the degree of specialization and SRS (figure S6). When using the first quartile of the global mainland species pool of hummingbirds rather than the first quartile of our dataset as a threshold to define smaller-ranged species (figure 3): (*i*) a logistic regression confirmed that the association between specialization and SRS remained significantly positive (R^2 = 0.345, P < 0.001, n = 46; figure 3*a*); (*ii*) a one-way ANOVA test showed significantly higher degree of specialization in communities with smaller-ranged species present (F = 6.719 , P = 0.013, n = 46; figure 3*b*) and; (*iii*) a linear regression conducted only for communities containing smaller-ranged species showed similar trend towards increased specialization in communities with higher proportion of smaller-ranged species (F = 6.739, P = 0.032, n= 10, R^2 = 0.457; figure 3*c*). Finally, null model corrected SRS remained significantly positively associated to specialization (R^2 = 0.357, P < 0.001, n = 46; figure 4), indicating that the influence of biome or continental narrowness on the range size of species is negligible in respect to the association between SRS and specialization.

4. Discussion

For hummingbird–plant networks across mainland Americas, we found that communities with high proportions of smaller-ranged species (SRS) also have a high degree of ecological specialization (figure 1-2). The association between SRS and specialization was insensitive to the definition used for smaller-ranged species (figure 3; S6), to the influence of biome or continental narrowness as accounted for by null models (figure 4), to the influence of species richness and network asymmetry on specialization (figure S3-S4) as well as how historical climate stability is summarised (figure S5). Although contemporary and historical climate was important in predicting both SRS and specialization, it did not affect the strong association between specialization and SRS. Notably, current precipitation was strongly correlated with hummingbird specialization, possibly explained by either increased productivity and thus greater opportunities for specialization or lower importance of insects in comparison to hummingbirds as pollinators in more rainy conditions, thereby favouring hummingbird–plant specialization [5,68,69]. Interestingly, we found a strong consistent negative link from temperature seasonality to SRS (figure. 2) and, when accounting for the indirect effects of climate on specialization via SRS, a direct positive association of temperature seasonality on specialization appeared (figure 2*b*). This positive association has likewise been observed for frugivorous bird-plant networks, which could be explained by non-overlapping interactions arising from higher annual turnover in species composition in more seasonal environments [50]. A synthesis of the effects of topography and climate together with the much stronger effect of SRS on specialization than *vice versa* (*std coeff.* = 0.75 *vs. std coeff.* = 0.43), is in accordance with the hypothesis that climate may increase specialization through reduced annual species range dynamics [30,42], facilitating adaptation to local foraging niches. However, the direct association between niche breadth and climatically induced population dynamics still lacks sufficient support by empirical evidence [70]. In accordance with the contrary hypothesis, that less specific adaptations to local food resources may extend the range over which a species can occur

resulting in fewer smaller-ranged species in the more generalized communities, a positive direct link from specialization to SRS remained present in all SEM models. Thus, although we are able to confirm the hypothesised interrelatedness between SRS and specialization, we are with the present data unable to firmly identify the underlying mechanism causing this association or their causal relationships.

In addition to contemporary climate, we found correlations with the estimates of historical climate anomaly. However, their effects were less consistent in the follow-up analyses (figure S3-S5) than those of contemporary climate, which in our models showed higher and consistent importance in predicting the interrelatedness of SRS and specialization. This indicates that late Quaternary temperature stability may play a role, but a minor one compared to contemporary climate. Contradicting the suggested high importance of historical climate changes for species range dynamics [11,31], our results could indicate that annual-scale climate stability also has a considerable influence for the preservation of smaller-ranged species through time [42]. The observed positive link from precipitation anomaly to specialization could derive from historical increases in productivity ultimately facilitating specialization. In contrast, the positive association to SRS could be explained by recent speciation events following the onset of glacial cycles during the Late Pleistocene, where species repeatedly disperse and become isolated in a heterogeneous environment – e.g. on mountain tops [71] – see Garcia-Moreno *et al.* for an explicit example with hummingbirds [72]. Mechanisms, as the latter, related to the evolutionary history of species also operates on time scales beyond the last glacial maximum [11,42], and may influence the intercorrelation of richness of smaller-ranged species, high levels of specialization and high local speciation-low extinction. Therefore, in order to understand what causes communities consisting of mainly smaller-ranged species to be more specialized, one could test the hypothesis that specialized hummingbirds and their nectar-food plants have concerted demographic trends in more stable

environments, ranking from current seasonality to climates at deep-time evolutionary time-scales [73]. This could potentially identify the main mechanism and temporal scale facilitating specialization in communities consisting of mainly smaller-ranged species, which have lower dispersal ability and thus may depend more on nectar-food plants from the local flora.

Irrespective of the exact mechanism involved, the detected relationship between SRS and specialization has relevance for ecological and evolutionary theory regarding their respective geographical patterns. Specifically, it illustrates that interspecific interactions are of great importance to consider when studying biogeographical patterns on large geographical scales, at least for highly specialized systems such as hummingbird–plant communities. Our results also have implications for conservation of species engaged in mutualistic associations, especially as anthropogenic activity may impact mutualistic interactions [74], and cause pollinator and linked plant extinctions [75,76]. For instance, the strong link between SRS and specialization indicate that some communities may be fragile in multiple ways, both by having smaller-ranged species slow in tracking ongoing climate changes and by having species less prone in switching their interactions and at higher risk of secondary extinctions [30,31,77]

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Author contribution

JS wrote the manuscript, carried out all statistical analyses, participated in the design and coordination of the study; AMMG assembled the plant-hummingbird database; JVB and PKM collected field data and participated in the design of the study and drafted the manuscript; BS and MSc advised the statistical analyses; ACA, FPA, SMA, ACB, PCA, TTI, GK, CA, FMGLC, AOM, CGM, MAM, ACM, DNB, GMO, PEO, JFO, LCR, LRL, AMR, MS, AT, IGV, ZW, SW collected data; JF participated in the design of the study and made the painted illustrations, JCS and CR participated in the design of the study and helped draft the manuscript; BD participated in the design and coordination of the study and helped draft the manuscript. All authors critically revised and approved the manuscript.

Data accessibility

Location, network characteristics and SRS (the proportion of smaller-ranged species) values of each hummingbird-plant network is presented at table S1. Same dataset has also been used and described for the analyses in Martín González et al. [20]

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673 **Figures and tables**

674

675 **Figure 1**. Geographical pattern of specialization and the proportion of smaller-ranged species (SRS)
676 for 46 hummingbird communities across mainland Americas. The coloration of each circle on the
677 map indicates the degree of specialization in relation to the proportion of smaller-ranged species
678 (SRS); black indicates both high SRS and specialization, white conversely indicates both low SRS
679 and degree of specialization. Orange and blue indicate poorer correlation through either high SRS
680 or specialization, respectively. Note that some points have been slightly moved to avoid overlap.
681 SRS was arcsin square-root transformed to improve normality. Painted illustration shows three
682 hummingbird species from the Costa Rican highlands, where the network with the highest degree of
683 specialization and SRS is found in the data set (specialization = 0.782, SRS = 0.6). From above:
684 Volcano Hummingbird (*Selasphorus flammula*), White-bellied Mountain-gem (*Lampornis*
685 *hemileucus*) and Fiery-throated Hummingbird (*Panterpe insignis*). Painting by Jon Fjeldså.

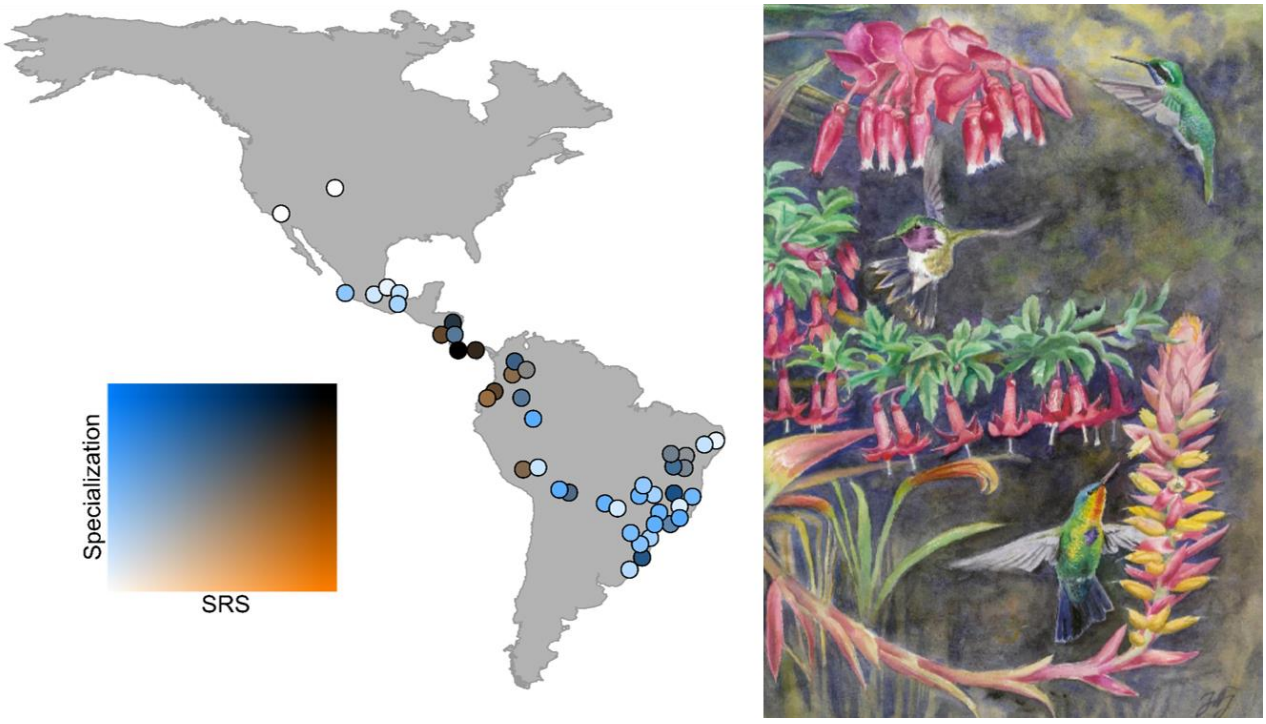

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Figure 2. Results from two reduced structural equation models showing the direct and indirect links of contemporary climate and Quaternary climate velocity on specialization and the proportion of smaller-ranged species (SRS; n = 46). *(a)* the path structure when specialization is hypothesized to predict of SRS. *(b)* the paths for the possible opposite scenario where SRS is hypothesized to predict specialization. Black arrows indicate positive relationships, red arrows indicate negative relationships; the thickness of each arrow illustrates the strength. The double headed grey arrows indicate covariance links. Other abbreviations are: MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality, PS, precipitation seasonality; AnomT, temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.

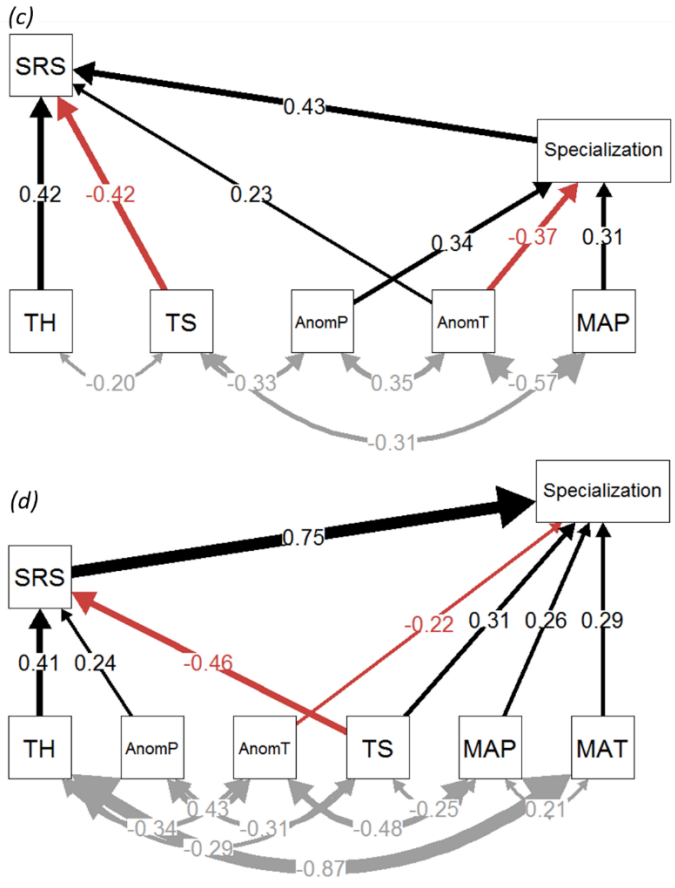


Figure 3. Three models constructed to test the relationship between specialization and a redefined measurement of the proportion of smaller-ranged species calculated based on the 1st quartile of the range-size frequency distribution for the global mainland species pool of hummingbirds (*n* = 318), rather than for the 130 species occurring in our data set. (*a*) Logistic regression testing the association between specialization and SRS when treating SRS as a binary variable (*n* = 46). (*b*) One-way ANOVA testing for difference in specialization among communities with smaller-ranged species either present or absent. (*c*) A linear regression testing the linear association between the proportion of smaller-ranged species (SRS) and specialization for communities with smaller-ranged species present (*n* = 10).

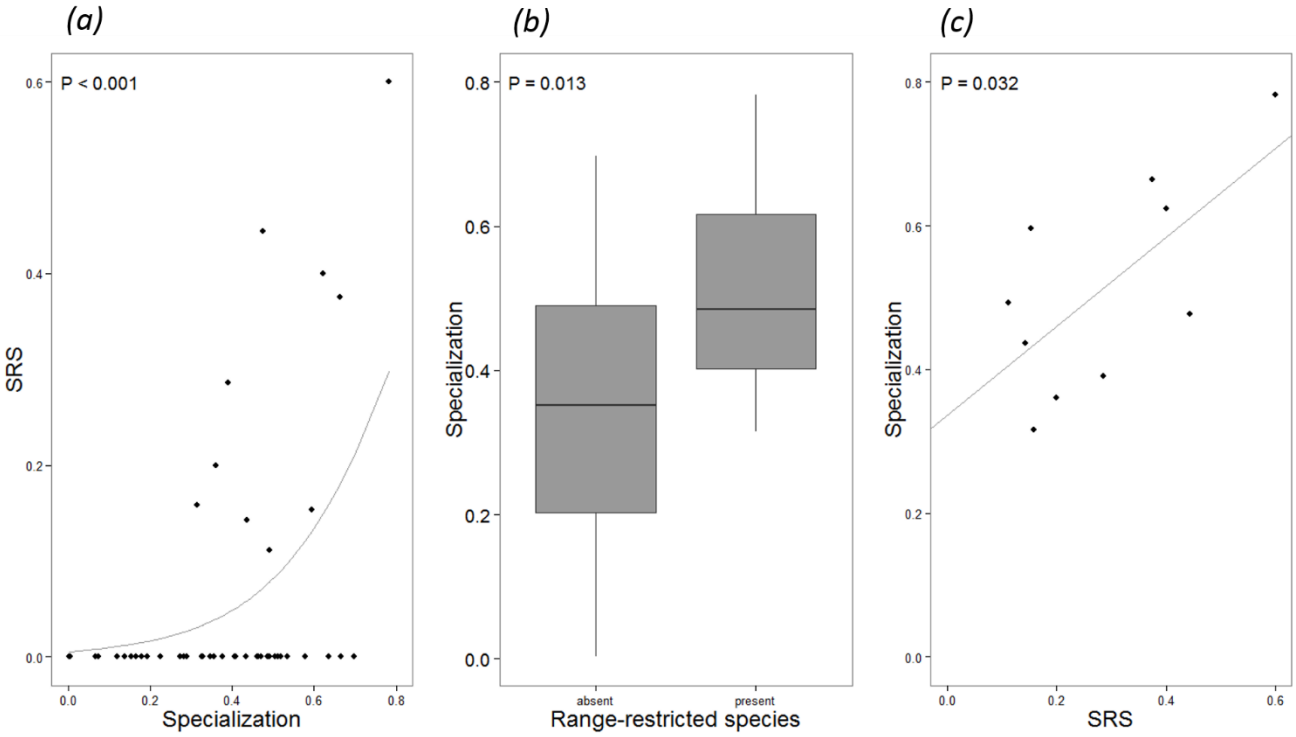
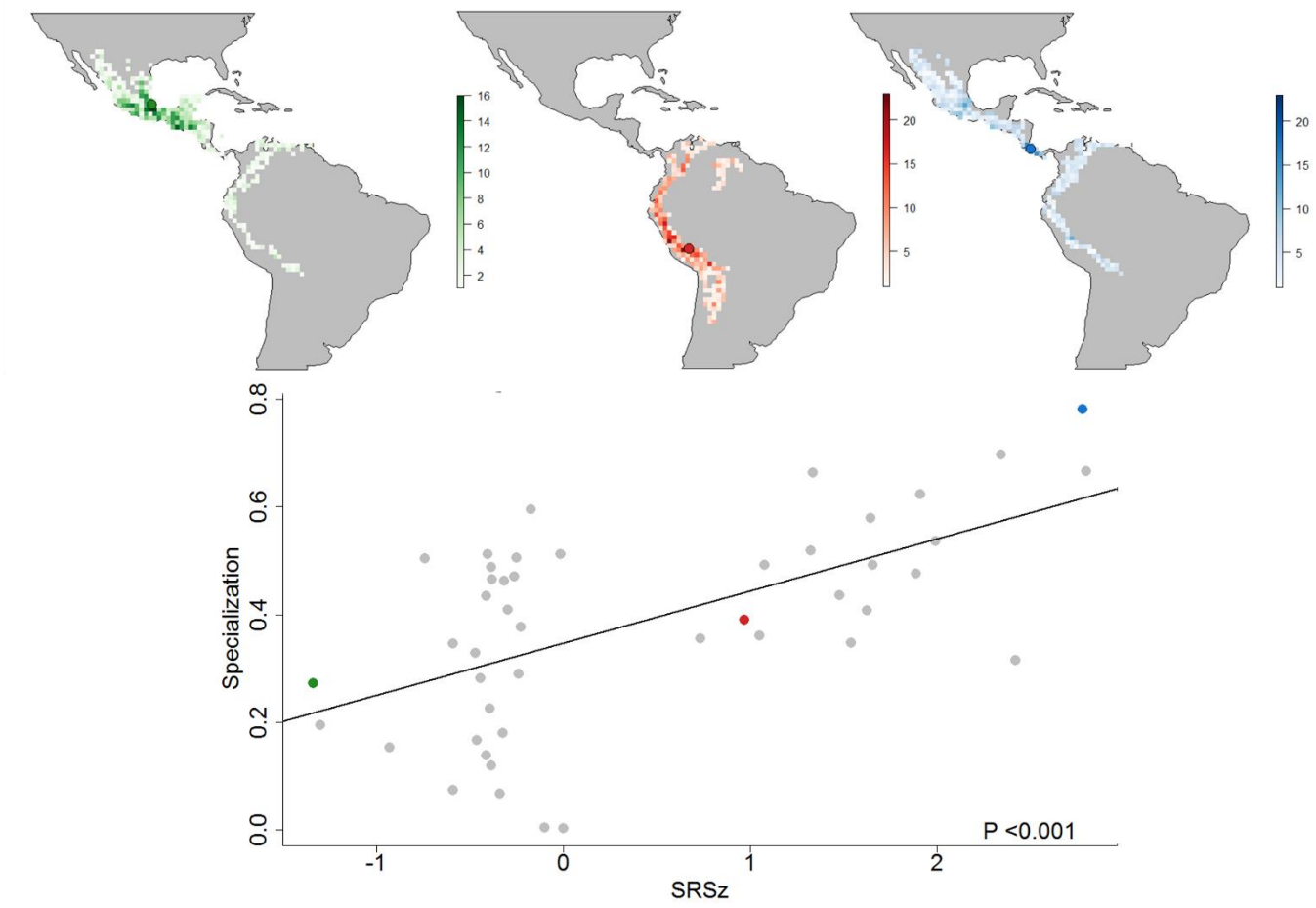


Figure 4. Scatterplot showing the correlation between specialization and a geographic null model correction of SRS. The source pool for each community was assembled using the rationale that species living in areas, which are compositionally more similar with the focal community, are more likely to be included (see Materials and Methods for details). Deviations between the observed SRS values and the normal curve of the null generated SRS values were standardized as the z-score. Maps show examples of the sampling frequency of grid cells for 1000 randomization within the hummingbird dispersion fields associated with each of the coloured example networks spanning the spectra of SRSz-scores.



Supplementary Material

Figure S1. Range size frequency distributions (RSFD) of all continental hummingbird species (*n* = 318*; a*) in comparison to the RSFS for continental hummingbird species occurring in the sampled communities *(n* = 130*; b*). The density indicate that all columns sum to one.

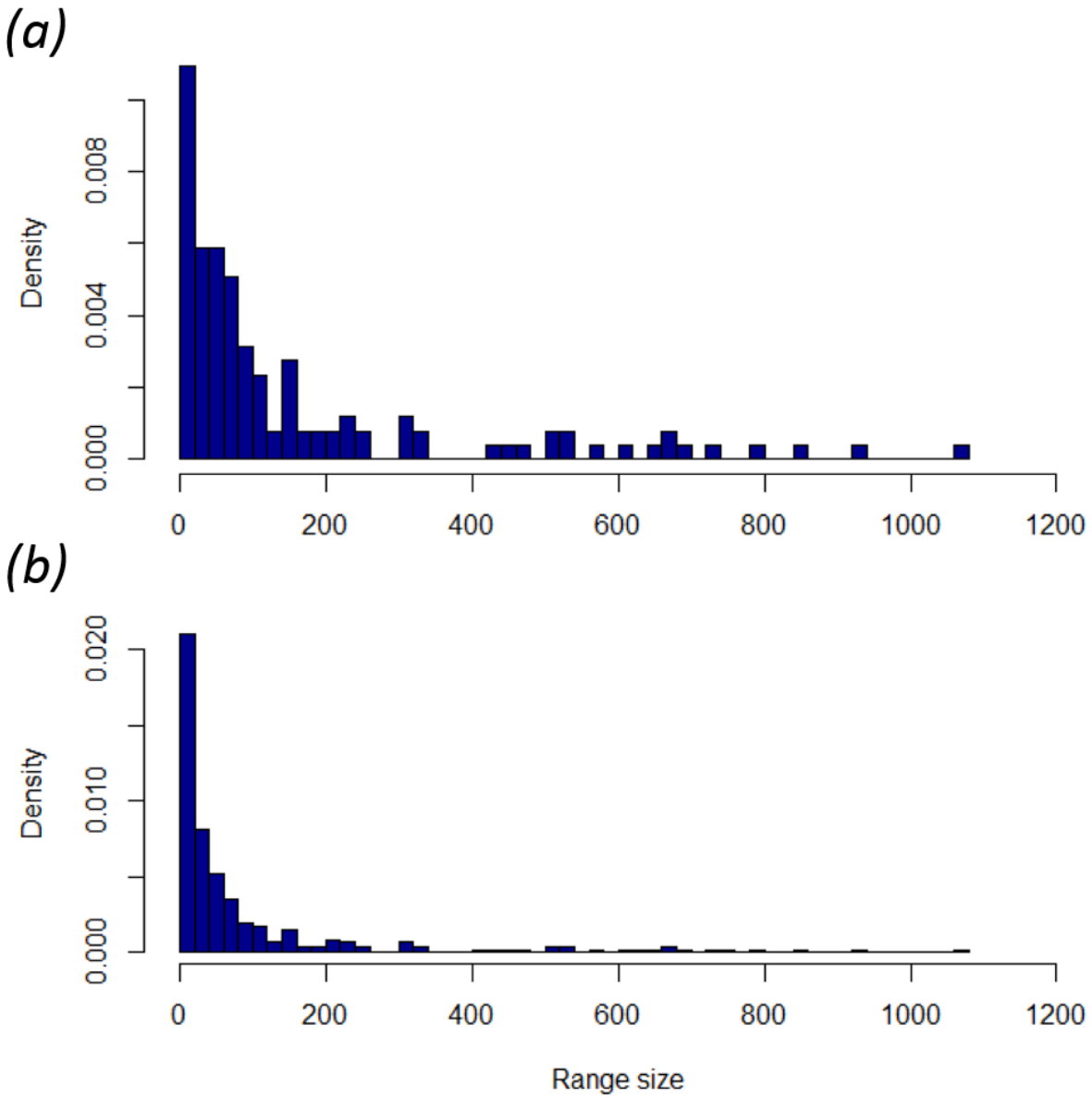


Figure S2. Initial structural equation models (SEMs) showing all direct and indirect effects of contemporary climate and Quaternary climate velocity on specialization and the proportion of smaller-ranged species (SRS; $n = 46$). *A* and *b* show initial SEMs including all predictors present in the best linear models (i.e. showing $\Delta AIC < 2$ in comparison to the model with lowest AIC). (*a*) a SEM predicting SRS through specialization and (*b*) *vice versa*. Error covariances were added to obtain appropriate fit (*see Materials and Methods*). Final SEMs with removed non-significant paths are presented in figure 2. Other abbreviations are: MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality, PS, precipitation seasonality; AnomT, temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.

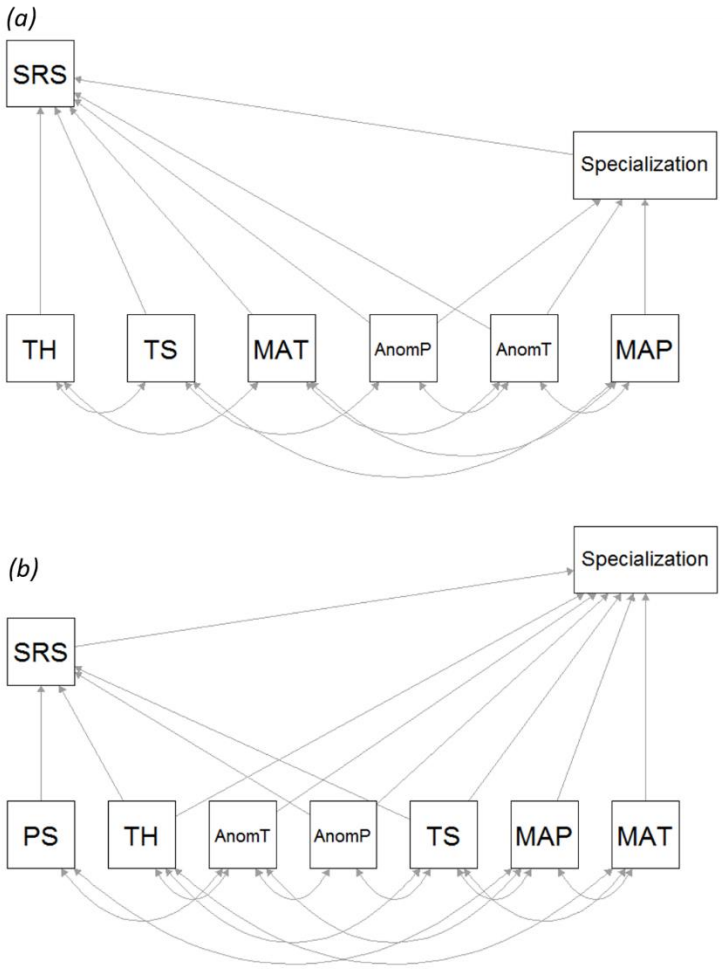


Figure S3. Results from two structural equation models, SEMs (n = 46), correcting specialization for the correlation with network size (i.e. the summed richness of plants and hummingbirds in the network). Similar to figure 2 and S2, *a* and *b* show initial SEMs including all predictors present in the best linear models (i.e. showing ΔAIC < 2 in comparison to the model with lowest AIC). Here, a SEM predicting SRS through specialization (*a*) and *vice versa* (*b*). Error covariances, shown as double headed arrows, were added to obtain appropriate fit (*see Materials and Methods). c and d* show reduced versions of the same SEMs where non-significant links have been removed. Black arrows indicate positive relationships, red arrows indicate negative relationships; the thickness of each arrow illustrates the strength. Other abbreviations are: MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality, PS, precipitation seasonality; AnomT, temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.

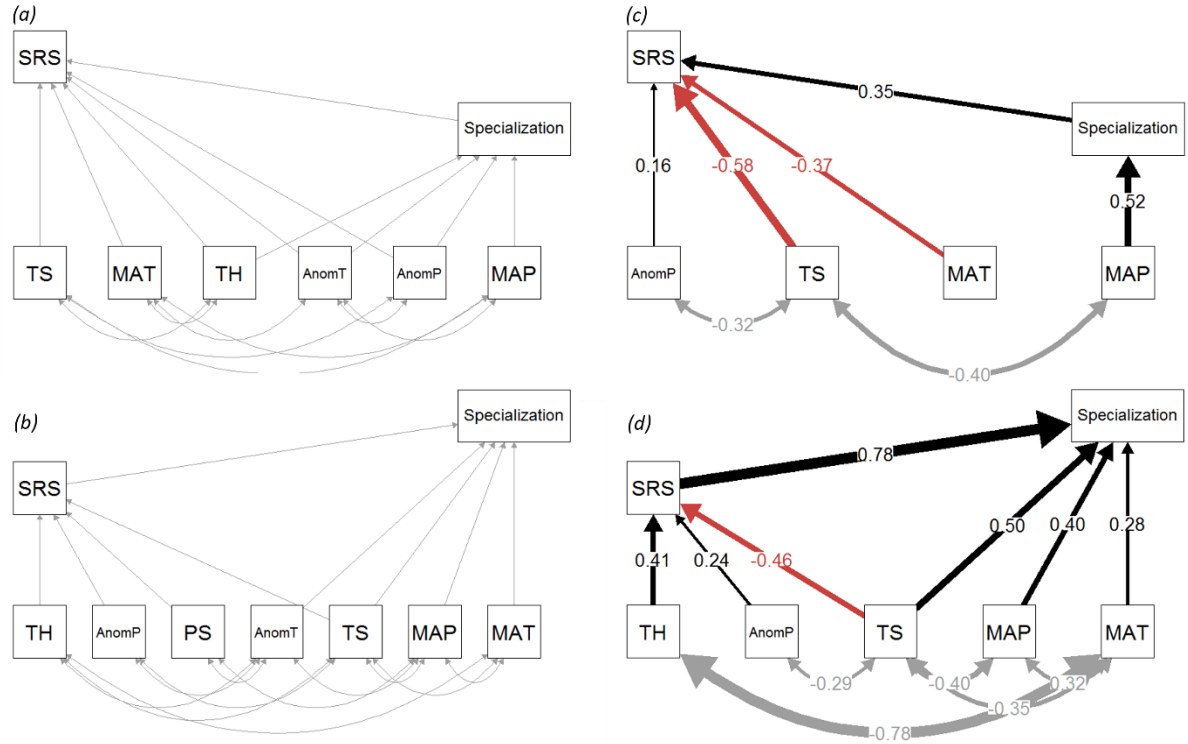


Figure S4. Results from two structural equation models, SEMs (n = 46), correcting specialization for the correlation with network asymmetry (i.e. the ratio between the network richness of hummingbird and plant species). Similar to figure 2 and S2-S3, *a* and *b* show initial SEMs including all predictors present in the best linear models (i.e. showing ΔAIC < 2 in comparison to the model with lowest AIC). Here, a SEM predicting SRS through specialization (*a*) and *vice versa* (*b*). Error covariances, shown as double headed arrows, were added to obtain appropriate fit (*see Materials and Methods). c and d* show reduced versions of the same SEMs where non-significant links have been removed. Black arrows indicate positive relationships, red arrows indicate negative relationships; the thickness of each arrow illustrates the strength. Other abbreviations are: MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality; PS, precipitation seasonality; AnomT, temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.

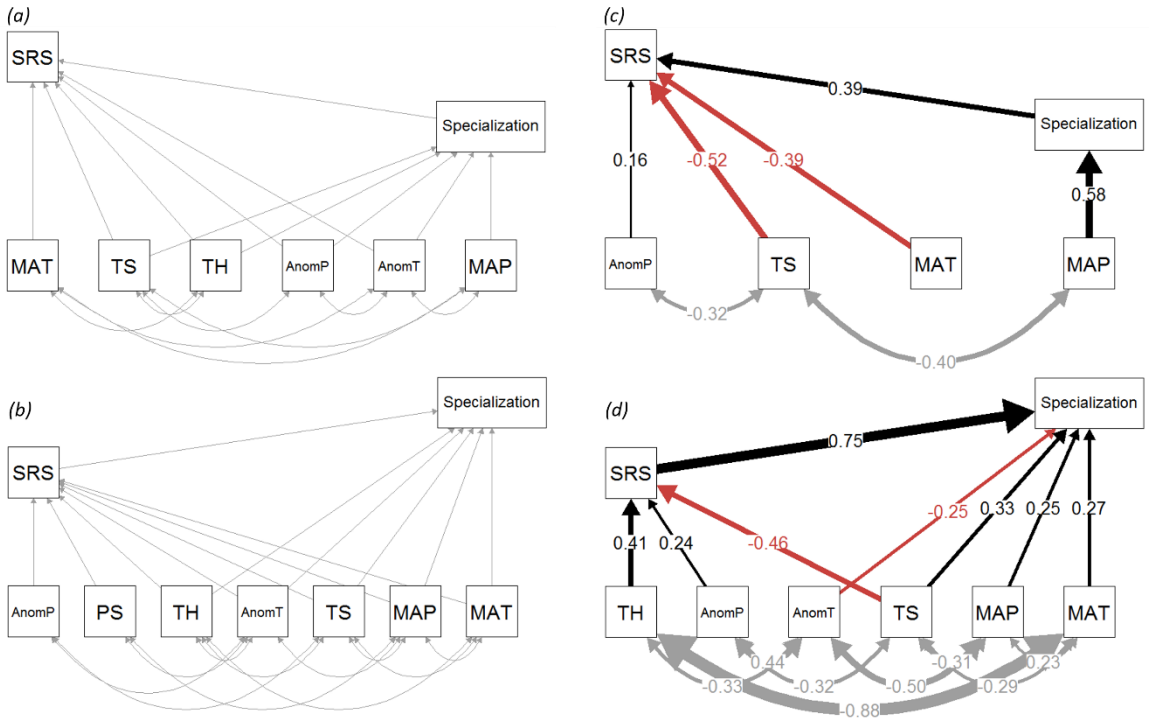


Fig. S5. Results from two structural equation models, SEMs (n = 46), considering the interactive effect of topography and historical climate change through estimates of temperature and precipitation velocity (VelT and VelP). Similar to figure 2 and S2-S4, *a* and *b* show initial SEMs including all predictors present in the best linear models (i.e. showing ΔAIC < 2 in comparison to the model with lowest AIC). Here, a SEM predicting SRS through specialization (*a*) and *vice versa* (*b*). Error covariances, shown as double headed arrows, were added to obtain appropriate fit (*see Materials and Methods). c and d* show reduced versions of the same SEMs where non-significant links have been removedved. Black arrows indicate positive relationships, red arrows indicate negative relationships; the thickness of each arrow illustrates the strength. Other abbreviations are: MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality, PS and precipitation seasonality.

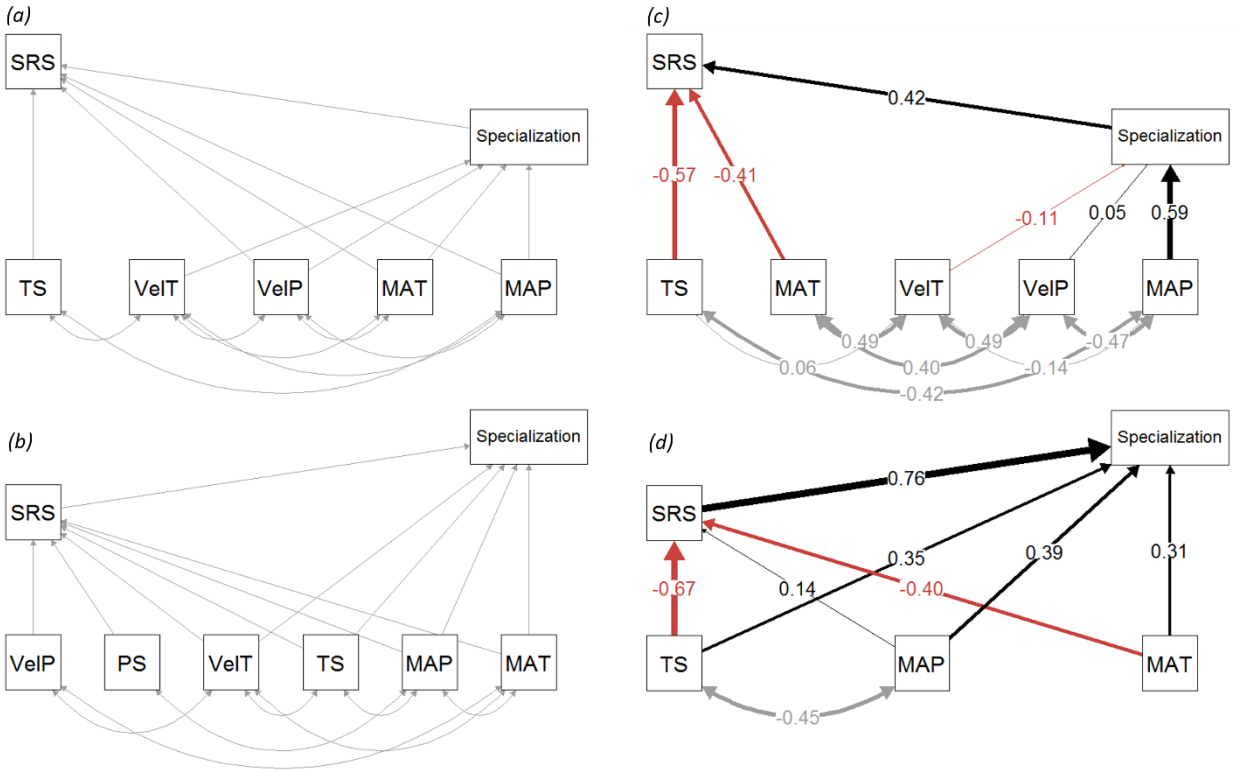


Fig. S6. Results from 10 linear models predicting the degree of specialization by the proportion of smaller-ranged species (SRS) calculated by considering cut-offs from 20-30% of the species data with the smallest range sizes. The black line indicate the 25% cut-off, which has been used to calculate SRS for the structural equation models (figure 2, S2-S5). Among the 10 regression models, the slope ranged from 0.33-0.39 (standard deviation = 0.02). all models were significant at 0.001 level.

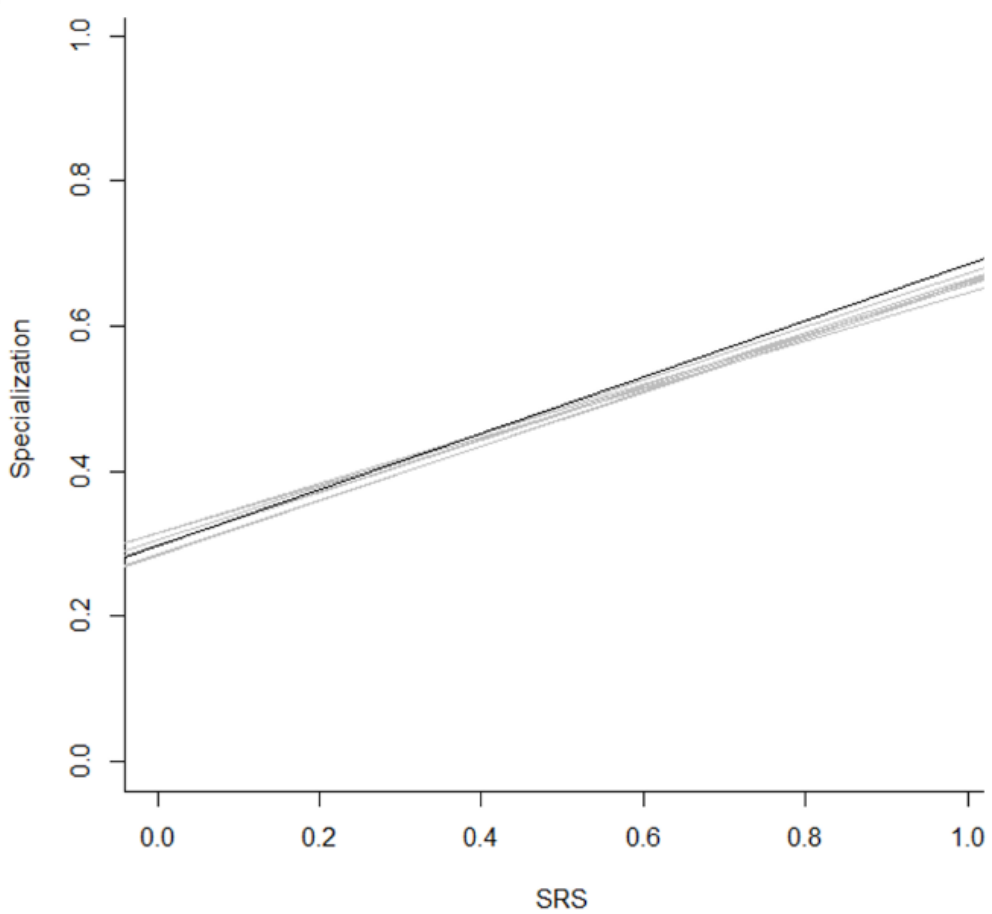


Table S1. Location, network size (total species richness), specialization (<d'>), SRS (the proportion of smaller-ranged species) of the plant-hummingbird networks and null model corrected SRS (SRSz; see material and method section for algorithmic details).

Network ID	Site	Latitude	Longitude	Network Size	Specialization	SRS
1	Atlantic forest, SE Brazil	-20.75	-42.92	22	0.43	0.00
2	Montane meadow, SW USA	34.22	-116.95	6	0.00	0.00
3	Sub-alpine meadow, Central USA	38.98	-106.97	4	0.01	0.00
4	Atlantic forest, SE Brazil	-23.35	-44.83	54	0.49	0.08
5	Tropical dry deciduous forest, W Mexico	19.5	-105.05	20	0.35	0.00
6	Pampa, S Brazil	-31.8	-52.42	35	0.23	0.00
7	Highland Atlantic forest, SE Brazil	-22.5	-44.83	37	0.46	0.00
8	Caatinga, NE Brazil	-7.87	-36.4	36	0.07	0.00
9	Altitudinal caatinga, NE Brazil	-11.48	-41.32	35	0.35	0.13
10	Amazonas riverine, SE Colombia	-3.82	-70.27	46	0.50	0.00
11	High andean forest, Colombia	1.25	-77.43	40	0.49	0.44
12	Atlantic Forest, low elevation	-27.27	-49.01	24	0.67	0.17
13	Atlantic Forest, mid elevation	-27.26	-49.02	14	0.29	0.00
14	Atlantic Forest, high elevation	-27.26	-49.02	11	0.38	0.00
15	Highland temperate mosaic forest, Central Mexico	19.23	-98.97	21	0.15	0.00
16	Suburban forest, Central Mexico	19.28	-98.23	10	0.07	0.00
17	Protected cloud forest, Central Mexico	19.5	-96.95	15	0.19	0.00
18	Rainforest, Colombia	0.07	-72.45	52	0.52	0.13
19	Caatinga forest, NE Brazil	-8.6	-38.57	11	0.18	0.00
20	Highland caatinga, NE Brazil	-13.12	-41.58	35	0.41	0.14
21	Open cerrado, NE Brazil	-13.12	-41.57	19	0.58	0.13
22	Campos rupestres, NE Brazil	-12.98	-41.33	42	0.44	0.14

Network ID	Site	Latitude	Longitude	Network Size	Specialization	SRS
23	Cloud forest, mid elevation, Costa Rica	10.27	-84.08	33	0.66	0.38
24	Cloud forest, high elevation, Costa Rica	10.18	-84.11	28	0.48	0.44
25	Cloud forest, low elevation, Costa Rica	10.44	-84.01	29	0.51	0.13
26	Cerrado, Central Brazil	-18.99	-48.3	25	0.28	0.00
27	Cerrado, Central Brazil	-19.16	-48.39	43	0.46	0.00
28	Cerrado, Central Brazil	-17.78	-48.68	21	0.33	0.00
29	Protected cloud forest, Central Mexico	19.5	-96.95	21	0.27	0.00
30	Pantanal wetland, SW Brazil	-19.52	-56.98	17	0.47	0.00
31	Campos rupestres, SE Brazil	-19.25	-43.52	56	0.70	0.17
32	Cerrado, W Brazil	-20.44	-54.65	20	0.14	0.00
33	Montane Forest, SE Brazil	-22.73	-45.58	31	0.49	0.00
34	Andean forest, Colombia	4.53	-73.85	22	0.36	0.33
35	Andean forest, Colombia	5.9	-73.42	34	0.60	0.17
36	Andean forest, Colombia	5.92	-73.53	19	0.36	0.17
37	Coastal cloud forest, SE Brazil	-23.63	-45.85	31	0.41	0.00
38	Primary forest, Bolivia	-17.51	-63.64	9	0.54	0.17
39	Primary forest, Bolivia	-16.96	-65.41	9	0.51	0.00
40	Campo rupestre, W Brazil	-19.95	-43.9	16	0.12	0.00
41	Atlantic forest, SE Brazil	-23.28	-45.05	56	0.51	0.00
42	Subtropical humid montane forest, Perú	-13.22	-72.12	12	0.39	0.33
43	Lowland primary forest, Perú	-12.85	-69.37	15	0.17	0.00
44	Andean rainforest, mid-elevation, Ecuador.	-0.02	-78.77	84	0.32	0.37
45	Elfin forest, Costa Rica	9.57	-83.73	22	0.62	0.50
46	Undisturbed highland páramo, Costa Rica	9.48	-83.48	30	0.78	0.60

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